Accepted: 18 January 2018

DOI: 10.1111/fwb.13082

ORIGINAL ARTICLE

WILEY Freshwater Biology

Shifts in mollusc traits following floodplain reconnection: Testing the response of functional diversity components

Andrea Rumm[1,2,3] | Francis Foeckler[2] | Frank Dziock[3] | Christiane Ilg[4] | Mathias Scholz[5] | Rebecca M. B. Harris[5,6] | Michael Gerisch[7]

[1]Institute of Biosciences, TU Bergakademie Freiberg, Freiberg, Germany

[2]ÖKON Ltd. Association for Landscape Ecology, Limnology, and Environmental Planning, Kallmünz, Germany

[3]Faculty of Agriculture/Environment/Chemistry, HTW Dresden, University of Applied Sciences, Dresden, Germany

[4]Hepia Geneva Member of the HES-SO University of Applied Sciences and Arts Western Switzerland, Jussy, Geneva, Switzerland

[5]Department of Conservation Biology, UFZ-Helmholtz Centre for Environmental Research, Leipzig, Germany

[6]Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC), University of Tasmania, Hobart, Australia

[7]Department of Animal Ecology, German Federal Institute of Hydrology—BfG, Koblenz, Germany

Correspondence
Andrea Rumm, ÖKON Ltd., Kallmünz, Germany.
Email: rumm@oekon.com

Funding information
Hanns-Seidel-Stiftung e. V.; Alexander von Humboldt-Stiftung

Abstract

1. Restoration of ecosystems can mitigate the global loss of biodiversity and provide essential ecological functions and services. Although trait composition and functional diversity (FD) are important tools in assessing recovery processes, very few restoration projects use them to evaluate restoration success. Consequently, little is known about trait and FD trajectories following restoration measures.
2. Here, we tested the effect of dyke-slotting to reconnect a floodplain on the trait response of mollusc communities over 6 years, based on a random stratified sampling design (plots within areas) with before and after control impact. Trait characteristics included flood resistance, drought resistance and resilience from which community-weighted mean trait values were derived. FD and its components (alpha, beta, gamma) were calculated with Rao's quadratic entropy.
3. Flood duration in the restored area increased from 4–13 to 6–17 weeks/year after reconnection, similarly to the reference area (4–10 to 6–14 weeks). Hence, the re-connection by dyke-slotting had no substantial effect on flood duration (due to seepage water).
4. Despite that, dyke-slotting triggered weak but significant shifts in the trait compositions of the restored floodplain mollusc communities. Traits reflecting species' resilience, crushing resistance and drought resistance increased in abundance, while traits characteristically found in more stable habitats decreased (e.g. cross-fertilisation, diet specialisation). Overall, trait composition of the restored area progressively moved to that found in the active floodplain.
5. While there were some significant temporal changes in FD within areas (reference, restored), there were no significant effects of dyke-slotting on any of the FD indices.
6. The incorporation of spatiotemporal dynamics of FD and trait composition may facilitate the evaluation of restoration trajectories, especially when different components (hierarchical FD configuration, single trait distributions) are considered together. Such complementary approaches could be integrated in future restoration monitoring programs.

KEYWORDS
floodplain, restoration, snails, spatiotemporal effects, species traits

1 | INTRODUCTION

The restoration of ecosystems can mitigate the global loss of biodiversity (Bullock, Aronson, Newton, Pywell, & Rey-Benayas, 2011). Restoration aims at recreating ecosystems with typical species compositions and processes that provide essential ecological functions and services. An important task of restoration ecology is the assessment of the spatiotemporal trends of biodiversity components to gauge restoration progress and success (restoration trajectories).

However, predicting where the desired target state will be reached, and how long it will take, is far from trivial, for several reasons. First, restoration progress is strongly determined by a multitude of ecological processes such as dispersal and inter-specific interactions, as well as by environmental heterogeneity or anthropogenic impacts like climate change and the spread of invasive species (Falk, Palmer, & Zedler, 2006). Additionally, monitoring is often based on short-term sampling of low spatial resolution, despite high environmental variability (Vaudor, Lamouroux, Olivier, & Forcellini, 2015). Finally, success in assessing and predicting restoration consequences can be limited by population characteristics such as temporal variation in abundance and small effect sizes of species' responses to restoration (Vaudor et al., 2015). Long-term monitoring with rigorous study designs (Vaudor et al., 2015) and the observation of different facets of diversity are crucial to estimate the success of restoration measures (e.g. Español, Gallardo, Comín, & Pino, 2015; Falk et al., 2006). Nevertheless, the implementation of such comprehensive studies is still rare and restoration success remains unclear (Suding, 2011).

The opening of dykes is increasingly seen as a successful restoration strategy for floodplains (Matella & Merenlender, 2014; Oppermann et al., 2009; Rumm, Foeckler, Deichner, Scholz, & Gerisch, 2016). The construction of dykes along large stretches of major rivers has isolated rivers from their floodplains (Matella & Merenlender, 2014), dramatically altering the driving processes induced by hydrology and hydrological connectivity (Tockner & Stanford, 2002). Consequently, up to 90% of Europe's floodplains are considered to be functionally degraded or lost (Tockner & Stanford, 2002). Re-establishing the connection between rivers and their adjacent sites is assumed to have numerous benefits, increasing the provision of floodplain ecosystem services (Oppermann et al., 2009) such as flood protection, water and nutrient supply, and wildlife habitat provision (Tockner, Lorang, & Stanford, 2010). The restored hydromorphological dynamics are assumed to initiate higher spatiotemporal habitat heterogeneity, extending the available total niche-space for species.

While in-stream restoration (e.g. flow restoration) or measures reconnecting aquatic floodplain habitats (like floodplain channels) are relatively well documented (e.g. Gallardo, Gascón, García, & Comín, 2009; Lamouroux, Gore, Lepori, & Statzner, 2015; and studies therein; Reckendorfer, Baranyi, Funk, & Schiemer, 2006), knowledge about the actual success of semi-terrestrial floodplain restoration measures is scarce, especially in terms of the functional effects on the plant and animal communities in those intermittent habitats (Español et al., 2015). It remains to be tested whether floodplain reconnection sustainably recovers communities with trait compositions typical for floodplain ecosystems.

Molluscs are excellent model organisms to test these questions. They are a species-rich group characteristic of riparian habitat settling in aquatic and terrestrial floodplain habitats and their transition zones. In naturally functioning floodplains, species are generally well adapted to frequent flooding and drought by behavioural, morphological, physiological or phenological features (e.g. possessing opportunistic life-history strategies: fast development, rapid reproduction, Adis & Junk, 2002; Lytle & Poff, 2004; Townsend & Hildrew, 1994). For the relatively immobile mollusc species, traits such as self-fertilisation, small shell size or vertical emigration are key adaptations enhancing species resistance or resilience to flooding (Funk, Schiemer, & Reckendorfer, 2013; Ilg, Foeckler, Deichner, & Henle, 2012; Plum, 2005; Reckendorfer et al., 2006). This leads to high taxonomical and functional similarity between floodplain communities (e.g. Kappes & Sulikowska-Drozd, 2016; Thomaz, Bini, & Bozelli, 2007).

Functional traits and their diversity are powerful tools indicating both the mechanisms driving community compositions after environmental changes and their subsequent effects on ecosystem processes (Mason & De Bello, 2013; Moretti et al., 2017). Response traits (i.e. Suding et al., 2008; e.g. reproduction mode) determine how species respond to changing habitat conditions and enable us to detect how communities are assembled, for example through habitat filtering or species interactions (Laughlin, 2014). The analysis of such relationships and processes offers great potential for restoration ecology, as it may provide important insights into the ecological mechanisms behind recovery patterns (Cadotte, Carscadden, & Mirotchnick, 2011; Laughlin, 2014). Nevertheless, restoration success is often assessed using taxonomic measures and few restoration studies apply trait-based approaches (e.g. Dolédec et al., 2015; Reckendorfer et al., 2006).

Functional diversity (FD) can be divided into alpha and beta components, providing important information about how, and on which scale, regional diversity (i.e. gamma diversity) is derived (Mason & De Bello, 2013). However, a decomposition of FD in alpha, beta and gamma diversity has only rarely been applied to assess restoration success (e.g. Paillex, Dolédec, Castella, Mérigoux, & Aldridge, 2013). This neglects important hierarchical, spatial and organisational scales on which FD operates and thereby can mask relevant patterns, especially along environmental gradients. This knowledge is necessary when selecting appropriate restoration measures and recreating processes typically driving floodplain biodiversity.

Here, we evaluated how dyke-slotting of a disconnected floodplain grassland affected the response trait composition and FD of the mollusc fauna by analysing spatiotemporal restoration trajectories. We expected (1) considerable turnover in the trait composition to occur following dyke-slotting because we expected large flooding changes in the restored floodplain. Traits affecting species resistance or resilience (e.g. strongly calcified shells, small shells) were expected to increase substantially in abundance, while other traits more

prominent in stable habitats (e.g. cross-fertilisation, diet specialisation) were expected to decrease. These trait changes were predicted to (2) shift the hierarchical FD components of the mollusc fauna. The restoration of hydromorphological dynamics was expected to allow more differentiated communities to coexist within a sampling plot (450–500 m^2, i.e. increasing alpha FD) and to enable new species/traits to establish in the restored floodplain, increasing its overall FD (i.e. gamma FD). We also expected FD turnover between mollusc communities (i.e. beta FD) to decrease.

2 | METHODS

2.1 | Study area and sampling

Mollusc sampling was part of an interdisciplinary study to monitor the restoration progress of one of the first dyke opening projects to be undertaken along the River Elbe in Germany (Scholz et al., 2009). The studied floodplain is located near the city of Dessau-Rosslau (Saxony-Anhalt, Elbe-km 253.0–257.5; Figure 1) within the UNESCO biosphere reserve "Middle Elbe/Elbe River Landscape." For almost 180 years, a 3.8-km-long dyke has divided the floodplain into two separate parts, isolating the areas behind the dyke from regular flooding (Scholz et al., 2009; Figure 1). Even though the area at the back of the dyke was cut off from flooding, it remained indirectly connected to river dynamics through seepage water. After opening the dyke at three locations, the 140 ha former floodplain behind the dyke was exposed again to flood dynamics. The first flooding since 1830 took place in spring 2009 (excluding extreme flood events in 1954, 2002).

To evaluate the restoration success of the dyke-slotting, a Before-After-Reference-Control-Impact monitoring design (Johnson, 2012; Lake, 2001) was implemented. An equally degraded (i.e. missing flooding) control area and a reference area not affected from the dyke-slotting and with similar habitat conditions to the impacted area were included to reveal whether the changes were caused by the restoration and to evaluate the progress towards the target state (Chapman & Underwood, 2000). Ideally, this monitoring design would use replicated areas, but this was not possible due to logistical and financial reasons, and because of the highly changeable hydrological regime of the Elbe within a few kilometres (see Rumm et al., 2016).

Here, the regularly flooded area on the riverside of the former dyke was included as reference (A in Figure 1), the area at the back of the dyke was the restored impacted area (B in Figure 1), and an inactive floodplain with an intact dyke close to the village of Klieken (Elbe-km 243.0–248.0) was selected as control area (C in Figure 1). Area C included two locally separated parts to provide sufficient plots with a similar range of site conditions as in the reference (A) and impacted (B) areas. Sampling areas were characterised by a mosaic of temporary waters and elevated plateaus with lower inundation frequency resulting in three different habitat types along the hydrological gradient: flood channels/depressions, wet grassland, mesophilous grassland. The frequency of grassland mowing is dependent on seasonal weather conditions (at most twice a year). For further details and discussion about areas, see Rumm et al. (2016).

Twelve plots were sampled within each area following a stratified randomised sampling design (described in more detail in Henle et al., 2006). Monitoring took place twice a year (spring, autumn)

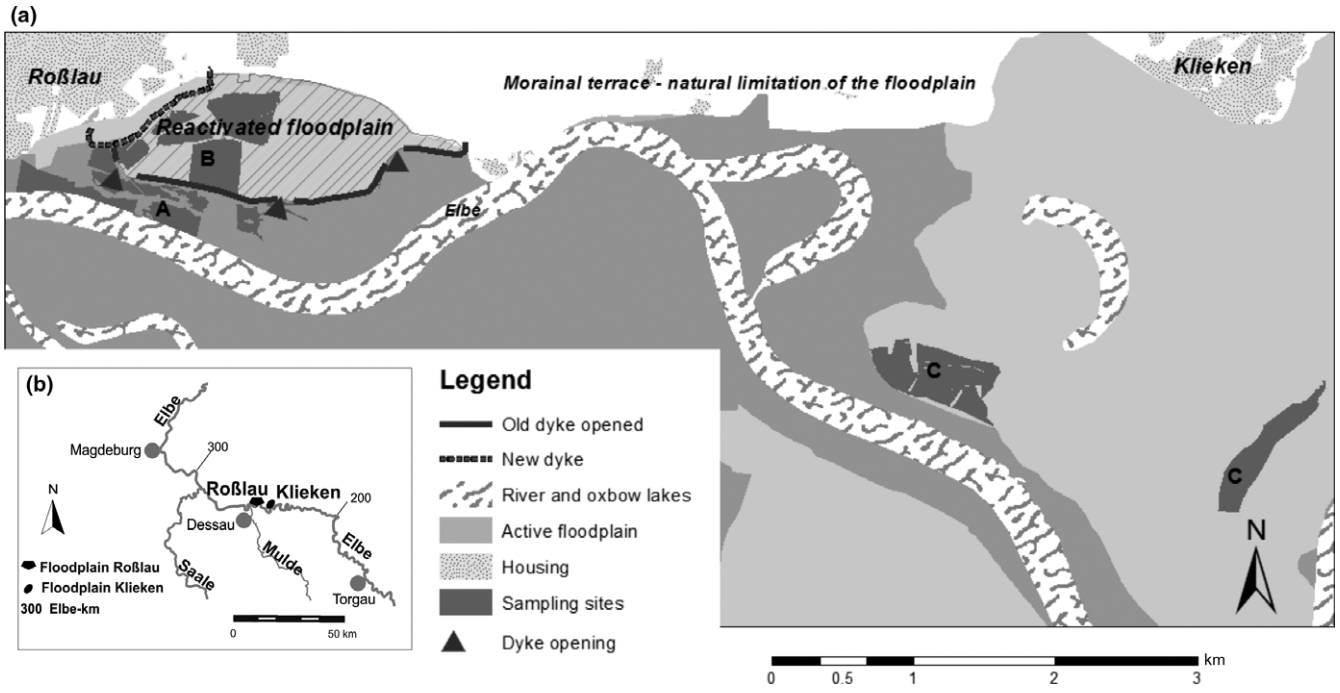

FIGURE 1 Sampling areas (a): reference (A), impacted (B), control (C) and location of the studied floodplain along the German Elbe (b; grey points represent nearby cities)

between autumn 2006 and autumn 2011, with the exception of 2008 when no flooding occurred. The 2006 and 2007 sampling seasons represent the status before dyke-slotting, and sampling from 2009 to 2011 represents the status after dyke-slotting.

Five soil samples together with their vegetation cover (0.1 m^2 × 5.0 cm) were taken with a spade from each plot to sample molluscs. When plots were flooded, samples were taken with a sieve (1.2-mm mesh size). To separate mollusc shells from plant and soil matter, the samples were prepared with a wet-sieving-vibrating machine (mesh sizes: 4.0, 2.0 and 0.7 mm). Mollusc shells were identified to species level where possible (Table S1) following the taxonomy and nomenclature of Körnig, Hartenauer, Unruh, Schnitter, and Stark (2013).

2.2 | Data analysis

2.2.1 | Data

In our data analyses, we only included molluscs that could be identified to at least genus level. A small number of mainly juvenile individuals (0.4% of the total) could only be identified to family level and were excluded (see Table S1). Mussels were not included (0.4% of the total number of individuals) because no trait information was available for these species.

To characterise trait composition and FD in the communities, 11 traits, which were only weakly correlated within species (pair-wise Spearman's rank-order correlation coefficients $\rho < .5$, Figure S1), with a total of 26 categories were included. These traits have been shown to be related to species resilience or resistance to the harsh environmental conditions of (semi-)natural floodplains found in both aquatic and (semi-)terrestrial habitats (frequent flooding, drought and their consequences; see Table 1). Trait information was obtained from the trait database of Falkner, Obrdlík, Castella, and Speight (2001), in which species-trait-associations are described by affinity scores using fuzzy-coding from zero (no affinity) to three (strong affinity; i.e. Chevenet, Dolédec, & Chessel, 1994). For taxa at the genus level, the trait values were calculated by averaging the affinity scores of all eligible species within the respective genus occurring in the regional species pool of the federal state of Saxony-Anhalt (Körnig et al., 2013). To weigh each species and trait equally, fuzzy-coded trait profiles were transformed into frequency distributions and the affinity scores standardised so that the sum for a given species and trait was equal to one (Statzner & Bêche, 2010). For example, an affinity score of three for large-sized shells and two for small-sized shells results in a frequency distribution of (3/5) = 0.6 and (2/5) = 0.4.

2.2.2 | Trait composition

To analyse the composition of response traits (subsequently called trait composition), community-weighted mean trait values (i.e. trait abundances) were calculated for each plot and season. They were computed as the average of trait values weighted by relative species' abundances in each trait category (following Garnier et al., 2004; Gayraud et al., 2003). Therefore, they represent the trait values of the dominant species in a community (Ricotta & Moretti, 2011).

2.2.3 | FD components

Following the approach of De Bello, Lavergne, Meynard, Lepš, and Thuiller (2010), FD was analysed on different hierarchical scales (alpha, beta, gamma) using Rao's quadratic entropy, summing up pair-wise trait dissimilarities weighted by relative species' abundances for each area and season. For trait dissimilarities, Gower distance was used to be more sensible to environmental filtering (De Bello, Carmona, Mason, Sebastià, & Lepš, 2013). Alpha FD was calculated as Rao's quadratic entropy of a community inhabiting a plot. Gamma FD refers to the total FD of an area, calculated in a similar way to alpha FD but taking into account communities of all plots within an area as one community. Beta FD is described as the average turnover of FD among the plots of an area and was calculated as the difference between gamma FD and mean alpha FD. As beta FD tends to be underestimated when alpha FD becomes larger (Jost, 2007), FD results were corrected based on the concept of "equivalent numbers" (Jost, 2007; according to De Bello et al. (2010), e.g. for alpha FD: $\text{alpha}_{\text{corrected}} = 1/[1 - \text{alpha}]$). This provides more ecologically meaningful and intuitively interpretable results (De Bello et al., 2010).

2.2.4 | Spatiotemporal trajectories

To analyse spatiotemporal variations within these indices, we used two approaches. First, we tested whether trait composition or FD was affected by the restoration measure using permutational analyses of variance with 9,999 permutations (PERMANOVA, Anderson, 2001). We used Gower distances calculated on multivariate community-weighted mean trait values to quantify differences in the overall trait composition between areas (control, impacted, reference) and over time (for the impacted area before and after dyke-slotting, respectively, for the control and reference area 2006–07 and 2009–11). Analogously, univariate PERMANOVAs were computed to analyse spatiotemporal variations within the community-weighted mean trait values of single trait categories and the FD components using Euclidean distances as dissimilarity metrics between observations. To deal with repeated-measurement over time, the plot number was included as a blocking factor. A significant interaction term between area and time was interpreted as an evident effect of the restoration measure.

To identify any change over time in the indices, we fitted linear mixed-effects models with restricted maximum likelihood estimation (except for gamma and beta FD, which were analysed by a simple linear model). As different patterns were assumed for different traits within areas, models were fitted for the community-weighted mean trait values of each trait category and in each area separately, following the protocol of Zuur, Ieno, Walker, Saveliev, and Smith (2009). The nine sampling seasons were set as a fixed factor, and plot number was included as a random effect to deal with repeated-measurement over time. An important assumption for linear mixed-effects

TABLE 1 Traits (according to Falkner et al., 2001) used to characterise the trait composition as well as FD in mollusc communities, their expected response to dyke-slotting (+ sign for abundance increase, − sign for abundance decrease) and assumed linkage to flood/drought resistance[c] and resilience[c] focusing on both aquatic and terrestrial floodplain molluscs. y, year

Trait categories (expected response)	Linked to[d]	Rationale explaining assumed linkage and expected response
Morphology		
Shell shape:		
Oblong shell (−); Globose/conical shell (−); Depressed shell (+)	Flood and/or drought resistance and/or resilience	Streamlined or flattened body shapes (cf. depressed shells) better resist water current (Townsend & Hildrew, 1994). Species with oblong or globose shells have to cope with higher torque (Heller, 1987), but can more effectively crawl up vertical vegetation or dig in the ground enduring flooding (and drought) in situ (Astor et al., 2014; Heller, 1987; Kappes & Sulikowska-Drozd, 2016; Poznańska et al., 2015)
Shell size:		
≤5 mm[a] (+); ≥5 mm[a] (−)	Flood resistance and/or resilience	Small shell sizes are linked to high passive dispersal capability allowing especially relative immobile species to (re-)colonise habitats effectively (Astor et al., 2014; Hausdorf, 2000; Ilg et al., 2012). Larger shells are more vulnerable to water current (Reckendorfer et al., 2006), getting caught more easily in branches and tree debris, and generally linked to less disturbed habitats (Townsend & Hildrew, 1994; Usseglio-Polatera et al., 2000)
Shell character:		
Poorly calcified shell (−); Strongly calcified shell (+)	Flood and/or drought resistance	Strongly calcified shells make molluscs more robust against crushing during dislodgement and minimise desiccation risk (Ilg et al., 2012; Poznańska et al., 2015)
Reproduction		
Reproduction mode:		
Cross-fertilisation (−); Self-fertilisation or parthenogenesis[a] (+)	Resilience	Uniparental reproduction mode provide reproductive assurance when mate number is reduced, for example due to adverse habitat conditions (Ilg et al., 2012; Plum, 2005; Pyron & Brown, 2015), and is assumed to be the fastest way to reproduce (Townsend & Hildrew, 1994)
Sexual maturity:		
<1 y (+); ≥1 y[a] (−)	Resilience	
Number of offspring:		
≤10 eggs[a] (−); ≥10 eggs[a] (+)	Resilience	Short (egg) development periods, early sexual maturity, high reproduction rates and short life span allow to re-establish populations rapidly after disturbances (Adis & Junk, 2002; Townsend & Hildrew, 1994; Usseglio-Polatera et al., 2000) being more dominant in flood-prone habitats (e.g. Fournier et al., 2012; Ilg et al., 2012)
Duration of egg development:		
Short: ≤2 weeks (+); Long: >2 weeks (−)	Resilience	
Longevity:		
<1 y (+); 1–2 y (+); ≥2 y (−)[a]	Resilience	
Oviposition:		
Calcified chorion (+); Capsule/egg mass (+); Ovo-viviparity (+); Soft chorion (−)	Flood and/or drought resistance	Ovo-viviparity or comparable protective oviposition strategies (at least in a broader sense, e.g. calcified chorions, egg mass) supply embryos with important nutrients (e.g. calcium), minimise dehydration risk and, therefore, favour a successful hatching under harsh habitat conditions (Baur, 1994; Heller, 1987; Ilg et al., 2012; Pyron & Brown, 2015). Also, egg mass (cf. cemented eggs) reduces mechanical stress (Gallardo et al., 2009; Townsend & Hildrew, 1994). Moreover, ovo-viviparity and egg mass enhance drift prevention (Funk et al., 2013). Unprotected clutches (cf. soft chorions) are linked to not-flooded sites (Gallardo et al., 2009)
Reproductive season[b]*:*		
Short: ≤6 months (+); Long: ≥7 months (−)	Resilience	Timing reproduction with the flow regime of the river, allows species to re-establish populations rapidly benefiting from the humidity after flooding (Hershkovitz & Gasith, 2013; Ilg et al., 2009; Lytle & Poff, 2004)

(Continues)

TABLE 1 (Continued)

Trait categories (expected response)	Linked to[d]	Rationale explaining assumed linkage and expected response
Food		
Diet specialisation[b]:		
Diet specialist: ≤3 food types; Generalist feeder: ≥4 food types	Resilience	High food supply features resilience (Hershkovitz & Gasith, 2013). Being able to utilise more than a few food types provides a clear advantage over diet specialists. Diet specialisation is more dominant in stable habitats (Usseglio-Polatera et al., 2000) where competitive exclusion is more likely to be found than in frequently disturbed ones (Townsend & Hildrew, 1994)

[a]Original trait categories were combined.
[b]To derive trait categories "duration of reproductive season" and "diet specialisation", for each taxon the number of affinity entries in the trait categories "main reproduction period", respectively, "food types" of Falkner et al. (2001) were counted.
[c]Definition follows Hershkovitz and Gasith (2013): resistance includes endurance (i.e. disturbance tolerance) and avoidance inclusive active and passive migration (drift) or emigration to refuges. Resilience is achieved by re-colonisation (migration, immigration) and/or reproduction.
[d]Traits cannot always be linked mutually exclusively to resistance or resilience (e.g. morphological features). Some traits contribute to both resilience and resistance (like size, Townsend et al., 1997; Townsend & Hildrew, 1994) or their linkages depend on the scale at which processes are viewed (Townsend & Hildrew, 1994). Moreover, traits supporting resistance (e.g. resting life forms) can also promote resilience, for example allowing species that remained on the site a rapid population re-establishment (Hershkovitz & Gasith, 2013).

models is normal distribution of the residuals and homogeneity of variances (Zuur et al., 2009). To account for the latter, we allowed different residual spreads within plots or sampling seasons by specifying a variance structure for one of these variables. Residuals of some models showed temporal correlation between sampling seasons, so we implemented a continuous-time-first-order autocorrelation structure. To decide whether the models had to account for different variances or correlation, we compared Akaike information criterion-values between models. Graphical inspection of standardised residuals was used to check the assumptions of our final models.

All analyses were carried out with the software R 3.3.1 (R Core Team, 2016) using the packages "FD" (Laliberté, Legendre, & Shipley, 2014), "vegan" (Oksanen et al., 2016), "nlme" (Pinheiro, Bates, DebRoy, & Sarkar, 2016), "lme4" (Bates, Maechler, Bolker, & Walker, 2015) and the function "Rao" (De Bello et al., 2010).

3 | RESULTS

3.1 | Flooding

Depending on the elevation, location and the habitat type, flood durations (determined by gauge) increased from 4–13 up to 6–17 weeks/year in the impact area after restoration (for more detailed results, see Rumm et al., 2016). The reference area was flooded for 4–10 weeks during 2006–08 and 6–14 weeks during 2009–11. The control area was influenced by seepage water for up to 3 or 5 weeks (2006–08, 2009–11, respectively) during monitoring. Consequently, the impacted (B) and control (C) areas were generally similar in terms of having no direct flooding (Rumm et al., 2016).

3.2 | Taxa

A total of 53 mollusc taxa (28 terrestrial and 25 aquatic) and 25,921 (8,338 terrestrial and 17,583 aquatic) individuals were included in the analysis. Four taxa, *Anisus leucostoma/spirorbis*, *Vallonia excentrica*, *Planorbis planorbis* and *Zonitoides nitidus* represented approximately 77% of the overall individual density (for a full taxa list see Table S1).

3.3 | Trait composition

Trait abundances differed significantly between the three areas ($p < .001$ for the "area"-term, Table 2). Moreover, significant spatiotemporal variations were found in trait abundances (Figure 2). Molluscs varied mainly in shell sizes ($p < .001$ for the "area"-term, detailed results for single traits are shown in Table S2), reproduction related traits (e.g. reproduction mode: $p < .01$, offspring number: $p < .001$, duration of reproductive season: $p < .001$), or diet specialisation ($p < .01$). However, some traits were equally distributed across the reference and impacted area (e.g. sexual maturity, egg number) and some traits (e.g. shell shape or character; Figure 2) did not differ between impacted, reference and control area.

3.4 | Trait trajectories after dyke-slotting

The dyke-slotting treatment effect on trait composition was highly significant but weak ($p < .001$ for the "area × time" interaction term, Table 2). Linear mixed-effects models showed substantial temporal increases or decreases in trait abundances (revealed by a significant slope in the models), predominantly in the mollusc community of the impacted area (in 16 of 26 trait categories). Fewer temporal changes were present in the trait composition of the other areas (three significant shifts in the reference and four borderline significant shifts in the control area, Figure 3). For example, after dyke-slotting, molluscs found in the impacted area had significantly smaller shell sizes ($p < .01$). Species with oblong shell shapes decreased substantially in abundances ($p < .05$) and more species possessed strongly calcified shells ($p < .01$). A higher proportion were able to reproduce by self-

TABLE 2 Results of PERMANOVAs calculated from multivariate community-weighted mean trait values and the hierarchical functional diversity (FD) components for the three studied areas (control, impacted, reference), time (before [2006–07] and after [2009–11] dyke-slotting) and plot number (except for beta and gamma FD only calculated at the area level); *df*, degrees of freedom; *F*, Fisher's univariate *F*-statistic; R^2, regression coefficient; *p*, *p*-values

Source of variation	Community-weighted mean trait values				Alpha FD				Beta FD				Gamma FD			
	df	*F*	R^2	*p*	*df*	*F*	R^2	*p*	*df*	*F*	R^2	*p*	*df*	*F*	R^2	*p*
Area	2	61.241	.180	***	2	2.173	.009	***	2	3.566	.237	*	2	6.889	.273	**
Time	1	0.593	.001	n.s.	1	13.613	.028	***	1	0.660	.022	n.s.	1	10.769	.213	**
Plot	33	8.769	.425	***	33	6.239	.429	***								
Area × time	2	7.971	.023	***	2	1.868	.008	n.s.	2	0.676	.045	n.s.	2	2.452	.097	n.s.

*$p < .05$, **$p < .01$, ***$p < .001$, n.s., not significant.

fertilisation or parthenogenesis ($p < .05$), during a shorter reproductive season ($p < .001$), and with shorter egg development time ($p < .01$). Furthermore, significant changes were revealed in the diet specialisation of species. Generalist feeders among molluscs seemed to profit from the dyke-slotting showing an abundance increase over time ($p < .01$). In contrast, diet specialists decreased in abundances ($p < .01$; for detailed results of linear mixed-effects models see Table S3).

3.5 | FD trajectories after dyke-slotting

While there were some significant temporal changes in the impacted area, there were no significant effects of dyke-slotting on any of the FD indices (Table 2). Alpha FD increased significantly in the impacted area after restoration ($p < .01$, Figure 4; for detailed results see Table S4), with the exception of a slight drop in the season following the first flooding (autumn 2009, Figure 5). Moreover, a borderline significant higher gamma FD was found in the impacted area ($p < .1$, Figure 4). In contrast, despite temporal variations over time (Figure 5), no significant changes were found in the FD components of the reference and control area ($p > .1$, Figure 4). At all three areas, mainly diverse communities on the plots (alpha FD) contributed to FD of an area (gamma FD), while the turnover between plots (beta FD) played a minor role (about 14.2%–21.5% of gamma FD, Table 3).

4 | DISCUSSION

4.1 | Effects of the dyke-slotting on the trait composition

Only minor changes in flood duration were visible after dyke-slotting because the impacted area has always been influenced by seepage water. Despite that, trait shifts in the impacted area were beyond the seasonal patterns that are typically present in (semi-)natural floodplains of the Elbe River and reflected recovery following dyke-slotting. In intact floodplains, mollusc communities often vary at the same place according to the specific hydrology of the sampling period (Foeckler, Schmidt, & Herrmann, 2010) as shown by the few significant temporal changes in the reference area. In contrast, the inactive area (control) offers the most stable habitat conditions and lacks substantial temporal trait variations.

Environment is expected to filter trait composition by modifying proportions rather than their range (De Bello, Dolezal, Ricotta, & Klimešová, 2011). Our results corroborate this. Dyke-slotting did not exclude traits completely or introduce new ones, but shifted trait profiles from single, highly dominant categories to a more balanced distribution of characteristics within traits (e.g. shell size). As also shown by Gallardo et al. (2009), a few trait features were extremely dominant in areas without flood dynamics (here, e.g. mainly large-sized species in the impacted area before restoration). This is in line with the theory that similar habitat conditions lead to high trait convergence among species (De Bello et al., 2011). However, in active floodplains, trait compositions vary considerably along the hydrological gradient with contrasting differences at the two extremes (Ilg et al., 2012; Paillex, Dolédec, Castella, & Mérigoux, 2009; Reckendorfer et al., 2006). This leads to more equally distributed trait characteristics (e.g. small- and large-sized species) in the reference and the impacted area after dyke-slotting.

In particular, traits closely linked to the effects of flood-disturbed or river-connected sites (see Table 1 for an overview) shifted after dyke-slotting. Before dyke-slotting, trait composition in the impacted area was dominated by large shells, narrow diet niches, cross-fertilisation and no timed reproductive season, reflecting the benign, stable and predictable habitat conditions (Gallardo et al., 2009; Lytle & Poff, 2004; Townsend & Hildrew, 1994; Usseglio-Polatera, Bournaud, Richoux, & Tachet, 2000). After dyke-slotting, abundances of these traits generally decreased significantly. Coincidentally, and as expected, traits linked to habitats with higher disturbance level (e.g. small shells, depressed shapes, self-fertilisation, generalist feeders; Finn & Poff, 2005; Gallardo et al., 2009; Townsend, Dolédec, & Scarsbrook, 1997) increased considerably as has been found in other floodplain restoration projects (e.g. Fournier, Samaritani, Shrestha, Mitchell, & Le Bayon, 2012). Timing of reproduction, a well-known strategy in floodplains where inundations occur mainly seasonally (Lytle & Poff, 2004), was also better synchronised with the flow regime of the Elbe River after dyke-slotting. This allows communities to (re-)establish rapidly, as humidity after floods reduces offspring

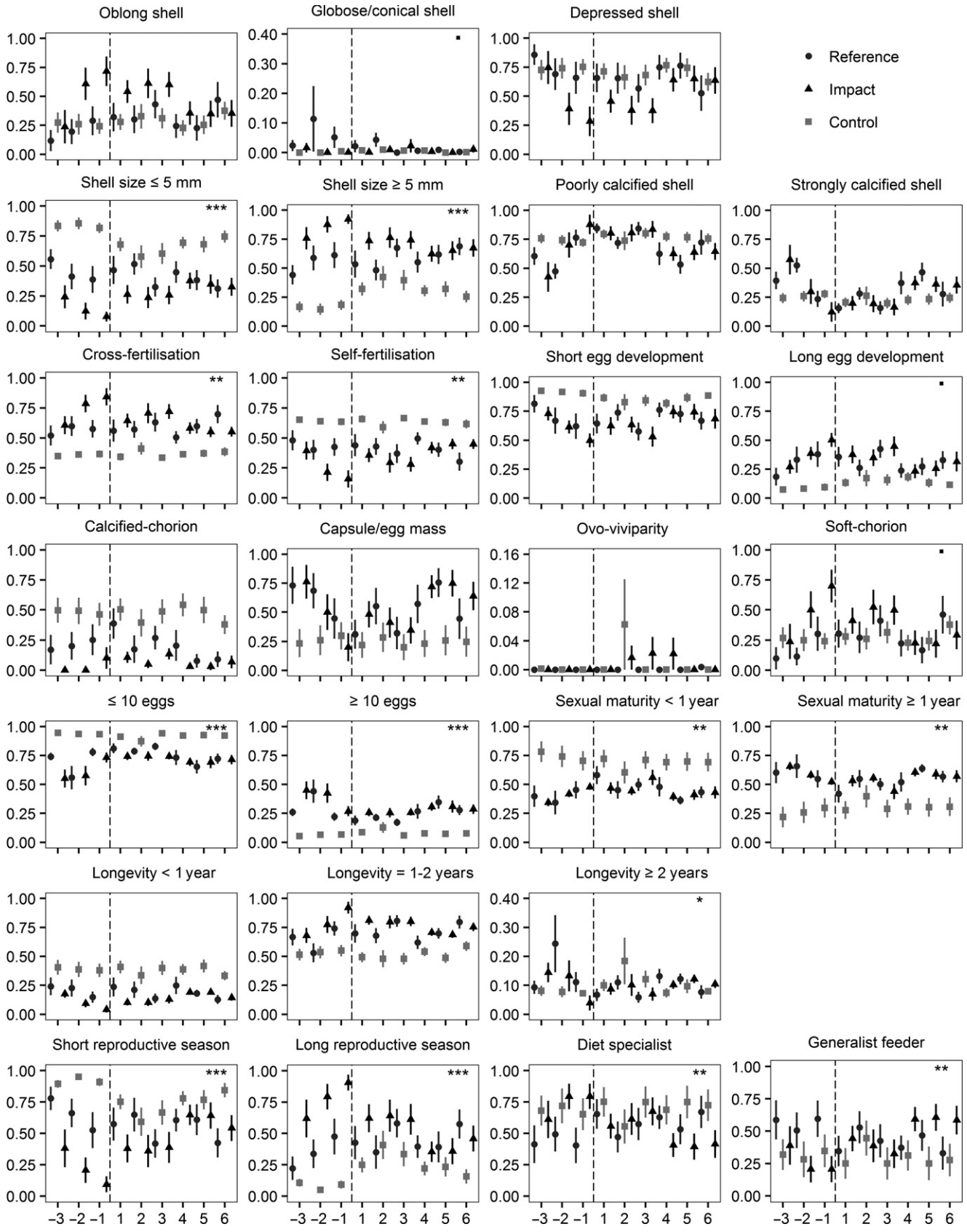

FIGURE 2 Spatiotemporal variations in trait abundances (means ± standard error of the mean) of the mollusc fauna in the three studied areas (control, impacted, reference) before (−3 to −1: 2006–07) and after (1–6: 2009–11; sampled twice a year in spring and autumn) dyke-slotting (vertical dashed line). Stars denote significance of area differences in trait abundances (***$p < .001$, **$p < .01$, *$p < .05$, .$p < .1$; for detailed results see Table S2)

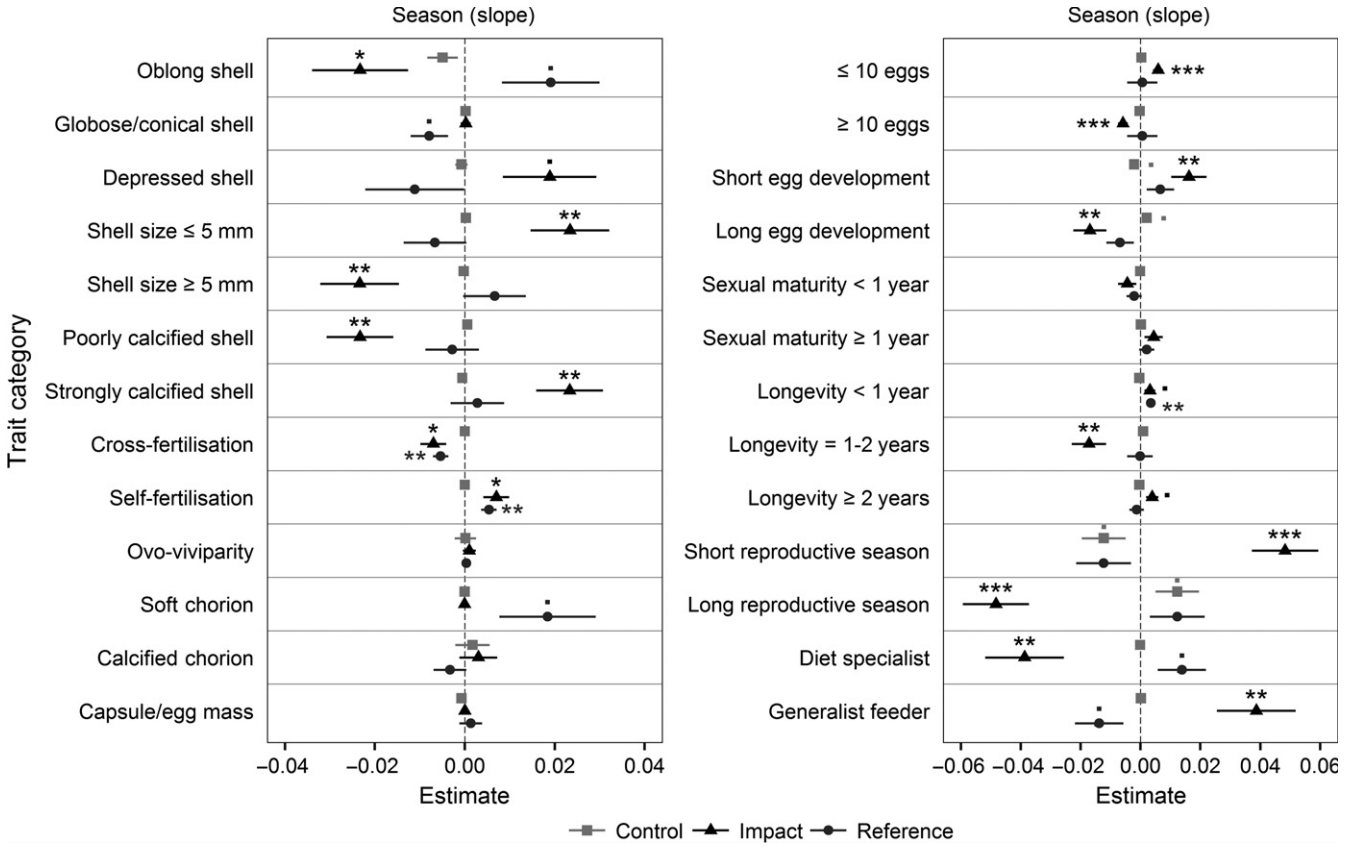

FIGURE 3 Slope (point symbols) and standard error (bars) of the linear mixed-effects models revealing temporal trends (i.e. increase or decrease) in trait abundances of the mollusc fauna in the three studied areas (control, impacted, reference). Slope values greater or smaller than zero show an increase or decrease in trait abundance over time. Stars denote significance (***$p < .001$, **$p < .01$, *$p < .05$, .$p < .1$; for detailed results see Table S3)

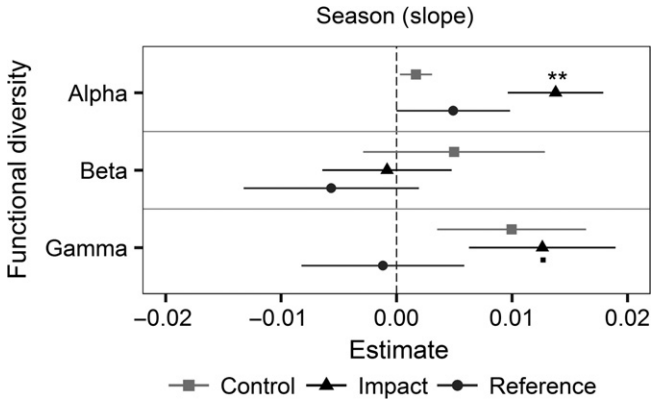

FIGURE 4 Slope (point symbols) and standard error (bars) of the linear mixed-effects models revealing temporal trends (i.e. increase or decrease) in the functional diversity (FD) of the mollusc fauna in the three studied areas (control, impacted, reference). Slope values greater or smaller than zero show an increase or decrease in FD over time. Stars denote significance (**$p < .01$, .$p < .1$; for detailed results see Table S4)

vulnerability risk (Hershkovitz & Gasith, 2013; Lytle & Poff, 2004). Moreover, (terrestrial) molluscs profit from the high passive concentration of potential sexual partners in floodplain depressions following flooding (Ilg, Foeckler, Deichner, & Henle, 2009).

The observed trait patterns suggest that molluscs do not respond to the dyke-slotting with an increase in "classical" flood resistance adaptations known from other species groups (i.e. drift prevention strategies, e.g. vertical emigration, suitable oviposition strategies, Table 1, Gallardo et al., 2009; Townsend & Hildrew, 1994). Instead, they appear to profit from resistance adaptations (e.g. strongly calcified/depressed shells) that minimise the risk of perishing during uncontrollable drift processes or unfavourable habitat conditions (mainly drought) and increase passive dispersal capability (e.g. smaller/depressed shells, Table 1). So molluscs cope with flooding following the "risk strategy" (i.e. Adis & Junk, 2002), using flood to colonise new habitats and to reproduce rapidly when habitat conditions are appropriate, as is also known from other species groups with low active mobility (e.g. meiofauna, Gaudes, Artigas, & Muñoz, 2010).

However, not all traits (e.g. longevity, shell character) responded to the dyke-slotting or were different between flooded and non-flooded areas. This could be due to several reasons. First, regional constraints (e.g. the low calcium content of the River Elbe) may affect trait distribution on a larger scale, while biotic interactions (e.g. competition, predation) influence smaller scale trait distribution. Second, there is a suite of traits enabling species to cope with particular habitat conditions (Townsend & Hildrew, 1994). These traits do not generally occur entirely within a species, but rather in

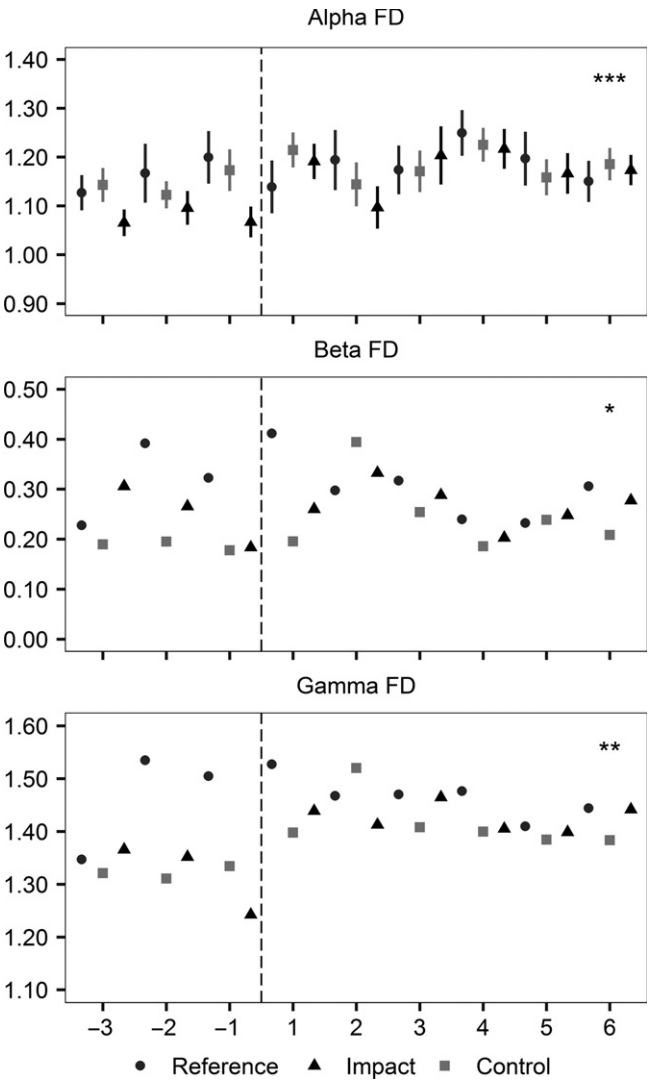

FIGURE 5 Spatiotemporal variations in the hierarchical functional diversity (FD) components (shown are means, and for alpha FD with ± standard error of the mean) of the mollusc fauna in the three studied areas (control, impacted, reference) before (−3 to −1: 2006–07) and after (1–6: 2009–11; sampled twice a year in spring and autumn) dyke-slotting (vertical dashed line). Stars denote significance of area differences in FD (***$p < .001$, **$p < .01$, *$p < .05$; for detailed results see Table 2)

combination with other traits that may be unrelated to disturbance (Finn & Poff, 2005). Additionally, traits are complex adaptation modes or life-history strategies that interact in different ways (e.g. through trade-offs among traits maximising species fitness, Verberk, Siepel, & Esselink, 2008). Finally, depending on the respective habitat conditions, traits may vary strongly within a mollusc species (i.e. intraspecific trait variability, e.g. smaller shells in fast-flowing areas; Pyron & Brown, 2015). This in turn can change their resistance or resilience potential (e.g. improved drought resistance, Poznańska, Kakareko, Gulanicz, Jermacz, & Kobak, 2015). It is not clear how much this has influenced the trait responses found here.

At the end of the monitoring, trait composition differed only between the active areas (reference, impacted) and the inactive floodplain (control). Again, this is consistent with other restoration studies (e.g. Paillex et al., 2009; Reckendorfer et al., 2006) and confirms that flooding is an important filter for floodplain trait compositions (Fournier, Gillet, Le Bayon, Mitchell, & Moretti, 2015; Gerisch, Agostinelli, Henle, & Dziock, 2012; Paillex et al., 2009; Poff, 1997). However, floodplains are subjected to many interacting human stressors (Tockner, Pusch, Borchardt, & Lorang, 2010) affecting trait compositions in different ways (Statzner & Bêche, 2010). For instance, flooding (here combined with seepage water behind the dyke, Rumm et al., 2016) and land-use intensity are closely related (e.g. Dziock et al., 2011; Foeckler, Deichner, Schmidt, & Castella, 2006). This most probably caused the contrasting differences in the trait composition of both areas situated at the back of the dykes (control, impacted before dyke-slotting). Less influenced by seepage water, the control area has been mown more frequently than the impacted area (Scholz et al., 2009). Mowing strongly and abruptly affects snails' microclimatic habitat conditions by inducing mechanical disturbance and high temperatures (Martin & Sommer, 2004). This encourages increased drought resistance potential (e.g. calcified eggs, Table 1). Adaptive trait strategies to land use are also known from other species groups, resulting in drastically different trait combinations between sites with different land-use intensity (e.g. Dziock et al., 2011; Gerisch et al., 2012).

TABLE 3 Overall functional diversity (gamma FD) of the three studied areas (control, impacted, reference) before (2006–07) and after (2009–11) dyke-slotting, partitioned into alpha and beta FD. For significance of changes within FD components after restoration, see Figure 4

Area	FD component	Before	After
Control	Alpha (% of gamma)	1.134 (85.8)	1.169 (82.6)
	Beta (% of gamma)	0.188 (14.2)	0.246 (17.4)
	Gamma	1.322	1.415
Impacted	Alpha (% of gamma)	1.068 (80.9)	1.159 (81.2)
	Beta (% of gamma)	0.252 (19.1)	0.268 (18.8)
	Gamma	1.320	1.427
Reference	Alpha (% of gamma)	1.148 (78.5)	1.165 (79.5)
	Beta (% of gamma)	0.314 (21.5)	0.301 (20.5)
	Gamma	1.462	1.466

4.2 | Effects of the dyke-slotting on FD

The rapid establishment of new species/traits led to an increased alpha FD and a slightly higher gamma FD after an initial, local loss of species/traits following dyke-slotting. Re-establishing hydromorphological dynamics in the impacted area apparently increased small-scale habitat heterogeneity (Rumm et al., 2016) and extended the available trait niche-space of the restored area, but responses were too weak to result in a significant treatment effect. Unexpectedly, beta FD did not change significantly, but tended to decrease, indicating a slightly higher trait similarity (i.e. smaller turnover) between communities.

Depending on the processes shaping community structures and their responses, changes of FD patterns in response to the same restoration can vary substantially between different taxonomic groups

(Fournier et al., 2015). Here, the high small-scale habitat heterogeneity allowed highly trait diverse species to coexist within a small area (i.e. individual plots) and led to high FD within mollusc communities, consistent with other mollusc studies (e.g. Astor et al., 2014). However, compared to the FD of individual communities (alpha FD), the turnover between communities (beta FD) was small, probably reflecting the short hydrological gradient sampled here. Combined with stochastic processes (dispersal), we suggest that niche differentiation and habitat filtering jointly explain the observed patterns, while shaping communities at different scales (as supposed by Poff, 1997). Locally, the high environmental heterogeneity typical of (semi-)natural floodplains allows very different species to co-occur within a small area (Ilg et al., 2009), resulting in high alpha FD. Coincidentally, habitat filtering leads to a high functional redundancy among mollusc communities (i.e. low beta FD), indicated by the dominance of predominantly similar trait strategies on the entire site (Villéger, Miranda, Hernandez, & Mouillot, 2012). In fact, the influence of the environment and spatial configuration on local and regional diversity depends on the time between flooding events (Funk et al., 2013; Kappes & Sulikowska-Drozd, 2016; Thomaz et al., 2007).

Overall, this confirms the importance of spatiotemporal variability in floodplain habitats caused by flooding dynamics. Nevertheless, on average, all three FD components of the control did not substantially differ from the flooded areas (reference, impacted after dyke-slotting). This is in line with other studies (Brinson, 1993; Gallardo et al., 2009), suggesting that communities inhabiting sites less or not affected by flooding are not less trait diverse per se, but that their traits are very different as floodplain characteristic molluscs were replaced by more drought tolerant, less disturbance adapted species (as shown here).

5 | CONCLUSIONS

To our knowledge, this is one of only a few studies (e.g. van Turnhout et al., 2012) analysing the effects of semi-terrestrial floodplain restoration using a standardised monitoring scheme with a relatively long time series. The results suggest a successful recovery has been initiated, with a mollusc fauna with trait features characteristic of floodplain grasslands being restored relatively quickly following dyke-slotting. Acting at different scales, niche differentiation and habitat filtering jointly explain FD and trait patterns found here. In particular, dyke-slotting increased the habitat niches at the small-scale allowing more flood-adapted species to coexist within the restored area. Our results emphasise the great opportunities offered by trait-based approaches for the ecological assessment of restoration processes (Dolédec et al., 2015; Laughlin, 2014). Considering shifts in different hierarchical FD components and trait composition together provided meaningful and comprehensive insights into restoration trajectories after dyke-slotting. FD alone would have been misleading as we did not find substantial differences in the hierarchical components between the inactive and active areas. More medium- to long-term studies, such as that presented here, will lead to greater insights and knowledge about which environmental conditions need to be altered in order for floodplain restoration to be successful.

ACKNOWLEDGMENTS

We are grateful to the administration of the UNESCO biosphere reserve "Middle Elbe," the nature conservation authorities and the farmers for their helpful cooperation. Furthermore, we would like to thank numerous colleagues from ÖKON (Kallmünz), the Helmholtz Centre for Environmental Research—UFZ (Leipzig) and the rangers of the Biosphere Reserve for their help in field work and sample preparation. Thanks to Oskar Deichner (Guteneck) for his support in identifying molluscs and Sarah Gwillym-Margianto for her assistance in proofreading. A.R. was supported by a grant from the Hanns-Seidel-Stiftung e.V. with funds from the German Federal Ministry of Education and Research. R.M.B.H. was supported by an Alexander von Humboldt research fellowship.

ORCID

Andrea Rumm http://orcid.org/0000-0002-7750-2063

REFERENCES

Adis, J., & Junk, W. J. (2002). Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: A review. *Freshwater Biology*, *47*, 711–731. https://doi.org/10.1046/j.1365-2427.2002.00892.x

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46.

Astor, T., Strengbom, J., Berg, M. P., Lenoir, L., Marteinsdóttir, B., & Bengtsson, J. (2014). Underdispersion and overdispersion of traits in terrestrial snail communities on islands. *Ecology and Evolution*, *4*, 2090–2102.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Baur, B. (1994). Parental care in terrestrial gastropods. *Experientia*, *50*, 5–14. https://doi.org/10.1007/BF01992042

Brinson, M. M. (1993). Changes in the functioning of wetlands along environmental gradients. *Wetlands*, *13*, 65–74. https://doi.org/10.1007/BF03160866

Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F., & Rey-Benayas, J. M. (2011). Restoration of ecosystems services and biodiversity: Conflicts and opportunities. *Trends in Ecology & Evolution*, *26*, 541–549. https://doi.org/10.1016/j.tree.2011.06.011

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Chapman, M. G., & Underwood, A. J. (2000). The need for a practical scientific protocol to measure successful restoration. *Wetlands*, *19*, 28–49.

Chevenet, F., Dolédec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, *31*, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

De Bello, F., Carmona, C. P., Mason, N. W., Sebastià, M. T., & Lepš, J. (2013). Which trait dissimilarity for functional diversity: Trait means or trait overlap? *Journal of Vegetation Science*, *24*, 807–819. https://doi.org/10.1111/jvs.12008

De Bello, F., Dolezal, J., Ricotta, C., & Klimešová, J. (2011). Plant clonal traits, coexistence and turnover in East Ladakh, Trans-Himalaya. *Preslia*, *83*, 315–327.

De Bello, F., Lavergne, S., Meynard, C. N., Lepš, J., & Thuiller, W. (2010). The partitioning of diversity: Showing Theseus a way out of the labyrinth. *Journal of Vegetation Science*, *21*, 992–1000. https://doi.org/10.1111/j.1654-1103.2010.01195.x

Dolédec, S., Castella, E., Forcellini, M., Olivier, J.-M., Paillex, A., & Sagnes, P. (2015). The generality of changes in the trait composition of fish and invertebrate communities after flow restoration in a large river (French Rhône). *Freshwater Biology*, *60*, 1147–1161. https://doi.org/10.1111/fwb.12557

Dziock, F., Gerisch, M., Siegert, M., Hering, I., Scholz, M., & Ernst, R. (2011). Reproducing or dispersing? Using trait based habitat templet models to analyse Orthoptera response to flooding and land use. *Agriculture, Ecosystems and Environment*, *145*, 85–94. https://doi.org/10.1016/j.agee.2011.07.015

Español, C., Gallardo, B., Comín, F. A., & Pino, M. S. (2015). Constructed wetlands increase the taxonomic and functional diversity of a degraded floodplain. *Aquatic Sciences*, *77*, 27–44. https://doi.org/10.1007/s00027-014-0375-2

Falk, D., Palmer, M. A., & Zedler, J. B. (2006). *Foundations of restoration ecology*. Washington, DC: Island Press.

Falkner, G., Obrdlík, P., Castella, E., & Speight, M. C. D. (2001). *Shelled Gastropoda of Western Europe*. Munich, Germany: Verlag der Friedrich-Held-Gesellschaft.

Finn, D. S., & Poff, N. L. (2005). Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology*, *50*, 243–261. https://doi.org/10.1111/j.1365-2427.2004.01320.x

Foeckler, F., Deichner, O., Schmidt, H., & Castella, E. (2006). Suitability of molluscs as bioindicators for meadow- and flood-channels of the Elbe-floodplains. *International Review of Hydrobiology*, *91*, 314–325. https://doi.org/10.1002/(ISSN)1522-2632

Foeckler, F., Schmidt, H., & Herrmann, T. (2010). Ökologische Untersuchungen im Isarmündungsgebiet. *BfN-Skripten*, *276*, 1–159.

Fournier, B., Gillet, F., Le Bayon, R.-C., Mitchell, E. A. D., & Moretti, M. (2015). Functional responses of multitaxa communities to disturbance and stress gradients in a restored floodplain. *Journal of Applied Ecology*, *52*, 1364–1373. https://doi.org/10.1111/1365-2664.12493

Fournier, B., Samaritani, E., Shrestha, J., Mitchell, E. A. D., & Le Bayon, R.-C. (2012). Patterns of earthworm communities and species traits in relation to the perturbation gradient of a restored floodplain. *Applied Soil Ecology*, *59*, 87–95. https://doi.org/10.1016/j.apsoil.2012.03.015

Funk, A., Schiemer, F., & Reckendorfer, W. (2013). Metacommunity structure of aquatic gastropods in a river floodplain: The role of niche breadth and drift propensity. *Freshwater Biology*, *58*, 2505–2516. https://doi.org/10.1111/fwb.12228

Gallardo, B., Gascón, S., García, M., & Comín, F. A. (2009). Testing the response of macroinvertebrate functional structure and biodiversity to flooding and confinement. *Journal of Limnology*, *68*, 315–326. https://doi.org/10.4081/jlimnol.2009.315

Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., … Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*, 2630–2637. https://doi.org/10.1890/03-0799

Gaudes, A., Artigas, J., & Muñoz, I. (2010). Species traits and resilience of meiofauna to floods and drought in a Mediterranean stream. *Marine and Freshwater Research*, *61*, 1336–1347. https://doi.org/10.1071/MF10044

Gayraud, S., Statzner, B., Bady, P., Haybachp, A., Schöll, F., Usseglio-Polatera, P., & Bacchi, M. (2003). Invertebrate traits for the biomonitoring of large European rivers: An initial assessment of alternative metrics. *Freshwater Biology*, *48*, 2045–2064. https://doi.org/10.1046/j.1365-2427.2003.01139.x

Gerisch, M., Agostinelli, V., Henle, K., & Dziock, F. (2012). More species, but all do the same: Contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos*, *121*, 508–515. https://doi.org/10.1111/j.1600-0706.2011.19749.x

Hausdorf, B. (2000). Biogeography of the Limacoidea sensu lato (Gastropoda: Stylommatophora): Vicariance events and long-distance dispersal. *Journal of Biogeography*, *27*, 379–390. https://doi.org/10.1046/j.1365-2699.2000.00403.x

Heller, J. (1987). Shell shape and land-snail habitat in a Mediterranean and desert fauna. *Biological Journal of the Linnean Society*, *31*, 257–272. https://doi.org/10.1111/j.1095-8312.1987.tb01992.x

Henle, K., Dziock, F., Foeckler, F., Volker, K., Hüsing, V., Hettrich, A., … Scholz, M. (2006). Study design for assessing species environment relationships and developing indicator systems for ecological changes in floodplains—The approach of the RIVA project. *International Review of Hydrobiology*, *91*, 292–313. https://doi.org/10.1002/(ISSN)1522-2632

Hershkovitz, Y., & Gasith, A. (2013). Resistance, resilience, and community dynamics in mediterranean-climate streams. *Hydrobiologia*, *719*, 59–75. https://doi.org/10.1007/s10750-012-1387-3

Ilg, C., Foeckler, F., Deichner, O., & Henle, K. (2009). Extreme flood events favour floodplain mollusc diversity. *Hydrobiologia*, *621*, 63–73. https://doi.org/10.1007/s10750-008-9632-5

Ilg, C., Foeckler, F., Deichner, O., & Henle, K. (2012). Hydrological gradient and species traits explain gastropod diversity in floodplain grasslands. *River Research and Applications*, *28*, 1620–1629. https://doi.org/10.1002/rra.1552

Johnson, D. H. (2012). Monitoring that matters. In R. A. Gitzen, J. J. Millspaugh, A. B. Cooper, & D. S. Licht (Eds.), *Design and analysis of long-term ecological monitoring studies* (pp. 54–73). Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9781139022422

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*, 2427–2439. https://doi.org/10.1890/06-1736.1

Kappes, H., & Sulikowska-Drozd, A. (2016). Heterogeneity of mollusc communities between and within forest fragments in a much modified floodplain landscape. *Folia Malacologica*, *24*, 9–24.

Körnig, G., Hartenauer, K., Unruh, M., Schnitter, P., & Stark, A. (2013). Die Weichtiere (Mollusca) des Landes Sachsen-Anhalt. *Berichte des Landesamtes für Umweltschutz Sachsen-Anhalt*, *12*, 1–336.

Lake, P. S. (2001). On the maturing of restoration: Linking ecological research and restoration. *Ecological Management and Restoration*, *2*, 111–115.

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12*. Available at: http://cran.r-project.org/web/packages/FD.

Lamouroux, N., Gore, J. A., Lepori, F., & Statzner, B. (2015). The ecological restoration of large rivers needs science-based, predictive tools meeting public expectations: An overview of the Rhône project. *Freshwater Biology*, *60*, 1069–1084. https://doi.org/10.1111/fwb.12553

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, *17*, 771–784. https://doi.org/10.1111/ele.12288

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, *19*, 94–100. https://doi.org/10.1016/j.tree.2003.10.002

Martin, K., & Sommer, M. (2004). Effects of soil properties and land management on the structure of grassland snail assemblages in SW Germany. *Pedobiologia*, *48*, 193–203. https://doi.org/10.1016/j.pedobi.2003.12.004

Mason, N. W. H., & De Bello, F. (2013). Functional diversity: A tool for answering challenging ecological questions. *Journal of Vegetation Science*, *24*, 777–780. https://doi.org/10.1111/jvs.12097

Matella, M. K., & Merenlender, A. M. (2014). Scenarios for restoring floodplain ecology given changes to river flows under climate change:

Case from the San Joaquin river, California. *River Research and Applications*, *31*, 280–290.

Moretti, M., Dias, A. T. C., De Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., … Berg, M. P. (2017). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*, 558–567. https://doi.org/10.1111/1365-2435.12776

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Minchin, P. R., … Wagner, H. (2016). *vegan: Community ecology package. R package version 2.4-1*. Available at: https://cran.r-project.org/web/packages/vegan.

Oppermann, J. J., Galloway, G. E., Fargione, J. E., Mount, J. F., Richter, B. D., & Secchi, S. (2009). Sustainable floodplains through large-scale reconnection to rivers. *Science*, *326*, 1487–1488. https://doi.org/10.1126/science.1178256

Paillex, A., Dolédec, S., Castella, E., & Mérigoux, S. (2009). Large river floodplain restoration: Predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology*, *46*, 250–258. https://doi.org/10.1111/j.1365-2664.2008.01593.x

Paillex, A., Dolédec, S., Castella, E., Mérigoux, S., & Aldridge, D. C. (2013). Functional diversity in a large river floodplain: Anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. *Journal of Applied Ecology*, *50*, 97–106. https://doi.org/10.1111/1365-2664.12018

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2016). *nlme: Linear and nonlinear mixed effects models. R package version 3.1-128*. Available at: https://cran.r-project.org/web/packages/nlme.

Plum, N. (2005). Terrestrial invertebrates in flooded grassland: A literature review. *Wetlands*, *25*, 721–737. https://doi.org/10.1672/0277-5212(2005)025[0721:TIIFGA]2.0.CO;2

Poff, N. L. (1997). Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, *16*, 391–409. https://doi.org/10.2307/1468026

Poznańska, M., Kakareko, T., Gulanicz, T., Jermacz, Ł., & Kobak, J. (2015). Life on the edge: Survival and behavioural responses of freshwater gill-breathing snails to declining water level and substratum drying. *Freshwater Biology*, *60*, 2379–2391. https://doi.org/10.1111/fwb.12664

Pyron, M., & Brown, K. M. (2015). Introduction to Mollusca and the class Gastropoda. In J. H. Thorp & D. C. Rogers (Eds.), *Ecology and general biology Thorp and Covich's freshwater invertebrates – Volume I* (pp. 381–421). London, UK: Academic Press.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reckendorfer, W., Baranyi, C., Funk, A., & Schiemer, F. (2006). Floodplain restoration by reinforcing hydrological connectivity: Expected effects on aquatic mollusc communities. *Journal of Applied Ecology*, *43*, 474–484. https://doi.org/10.1111/j.1365-2664.2006.01155.x

Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, *167*, 181–188. https://doi.org/10.1007/s00442-011-1965-5

Rumm, A., Foeckler, F., Deichner, O., Scholz, M., & Gerisch, M. (2016). Dyke-slotting initiated rapid recovery of habitat specialists in floodplain mollusc assemblages of the Elbe River, Germany. *Hydrobiologia*, *771*, 151–163. https://doi.org/10.1007/s10750-015-2627-0

Scholz, M., Rupp, H., Puhlmann, G., Ilg, C., Gerisch, M., Dziock, F., … Henle, K. (2009). Deichrückverlegung in Sachsen-Anhalt und wissenschaftliche Begleituntersuchungen am Beispiel des Rosslauer Oberluchs. *Naturschutz im Land Sachsen-Anhalt*, *Sonderheft*, *46*, 103–115.

Statzner, B., & Bêche, L. A. (2010). Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, *55*, 80–119. https://doi.org/10.1111/j.1365-2427.2009.02369.x

Suding, K. N. (2011). Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics*, *42*, 465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Suding, K. N., Lavorel, S., Chapin, III, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., … Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Thomaz, S. M., Bini, L. M., & Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, *579*, 1–13. https://doi.org/10.1007/s10750-006-0285-y

Tockner, K., Lorang, M. S., & Stanford, J. A. (2010). River flood plains are model ecosystems to test general hydrogeomorphic and ecological concepts. *River Research and Applications*, *26*, 76–86. https://doi.org/10.1002/rra.1328

Tockner, K., Pusch, M., Borchardt, D., & Lorang, M. S. (2010). Multiple stressors in coupled river–floodplain ecosystems. *Freshwater Biology*, *55*, 135–151. https://doi.org/10.1111/j.1365-2427.2009.02371.x

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. *Environmental Conservation*, *29*, 308–330.

Townsend, C. R., Dolédec, S., & Scarsbrook, M. R. (1997). Species traits in relation to temporal and spatial heterogeneity in streams: A test of habitat templet theory. *Freshwater Biology*, *37*, 367–387. https://doi.org/10.1046/j.1365-2427.1997.00166.x

Townsend, C. R., & Hildrew, A. G. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, *31*, 265–275. https://doi.org/10.1111/j.1365-2427.1994.tb01740.x

Usseglio-Polatera, P., Bournaud, M., Richoux, P., & Tachet, H. (2000). Biological and ecological traits of benthic freshwater macroinvertebrates: Relationships and definition of groups with similar traits. *Freshwater Biology*, *44*, 563–568.

van Turnhout, C. A. M., Leuven, R. S. E. W., Hendriks, A. J., Kurstjens, G., van Strien, A., Foppen, R. P. B., & Siepel, H. (2012). Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds. *River Research and Applications*, *28*, 269–282. https://doi.org/10.1002/rra.1455

Vaudor, L., Lamouroux, N., Olivier, J.-M., & Forcellini, M. (2015). How sampling influences the statistical power to detect changes in abundance: An application to river restoration. *Freshwater Biology*, *55*, 135–151.

Verberk, W. C. E. P., Siepel, H., & Esselink, H. (2008). Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology*, *53*, 1722–1738. https://doi.org/10.1111/j.1365-2427.2008.02035.x

Villéger, S., Miranda, J. R., Hernandez, D. F., & Mouillot, D. (2012). Low functional β-diversity despite high taxonomic β-diversity among tropical estuarine fish communities. *PLoS ONE*, *7*, e40679. https://doi.org/10.1371/journal.pone.0040679

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*, 1st ed. New-York, NY: Springer-Verlag. https://doi.org/10.1007/978-0-387-87458-6

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Rumm A, Foeckler F, Dziock F, et al. Shifts in mollusc traits following floodplain reconnection: Testing the response of functional diversity components. *Freshwater Biol*. 2018;63:505–517. https://doi.org/10.1111/fwb.13082